Support Information Appendix

Hamilton's inclusive fitness maintains heritable altruism polymorphism through *rb = c*

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Breeding social organizations across the animal kingdom: A perspective of altruism polymorphism

Reproductive altruism, with its critical influence on organisms' fitness, is the most prevalent and important form of altruistic behavior. As we have shown in the main text, the three evolutionary states of altruistic vs. non-altruistic genotypes — stable equilibrium, increasing or decreasing in frequency, which are respectively mediated by $rb = c$, $rb > c$ and $rb < c$ — all can be found from breeding social organizations across the animal kingdom. Here, based on this framework, we arrange both invertebrates and vertebrates along a continuum of social organizations in terms of altruism polymorphism. It is worth pointing out that this framework based on the rb vs. c relation is theoretical one, although in empirical studies the potential factors such as individual quality and ecological condition that affect the relation, and the potential mechanisms such as selection-mutation balance and negative frequency-dependent selection underlying the social polymorphisms, should be taken into account. We also compile information on inter-specific and intra-specific variation in breeding social organization. Furthermore, we clarify the conceptual difference between phenotype-based and genotype-based altruism polymorphism in the same population.

Our primary objective is to further illuminate why our synthesis can serve as a general guiding framework for understanding the evolution and maintenance of altruism in particular and sociality in general.

Breeding Social Organizations in the Animal Kingdom: Definition and Distribution. Levels of sociality associated with reproduction have been measured with diverse criteria and terminology (1, 2, 3, 4). Here we define breeding social organization from a perspective of altruism polymorphism at the population scale. First, we classify breeding units within the same population of a single species as solitary and cooperative. The former refers to a unit in which one or both of the pair members are solely responsible for rearing their own offspring, and the latter refers to a unit in which individuals additional to the pair members are involved in rearing offspring of the pair. By this definition, reproductive aggregations in which there is no alloparental care (e.g. colony-nesting waterfowl on island habitats) are excluded. Then, according to differential combinations of the two types of breeding units, we can classify breeding social organizations as solitary, facultative and eusocial, and arrange species or populations into one of the three types (Table S1, Figs. S1 and S2).

Solitary: All breeding units in a population are solitary. This type of breeding social organization is found in the majority of both invertebrate and vertebrate species. Such populations are more likely to be in monomorphic equilibrium and contain no altruistic genotype, which can be characterized by $rb < c$.

Facultatively cooperative (called as primitively eusocial in insects): Both solitarily and cooperatively breeding units coexist within the same population of a species. In such species, helpers (workers in insects) are usually close relatives of helped breeders. Helpers retain the potential ability to reproduce on their own, and do not differ from solitary or helped breeders in morphology, although they are often smaller and younger than the latter. Nevertheless, in a few tropical insects, for example the paper wasp *Ropalidia marginata*, cooperative groups contain helpers that stay at their natal nests and never become a queen for all of their lives (5).

This type of social organizations is exhibited by some insects and vertebrates. Cooperative groups often have higher productivity than independent breeders within the same population due to the presence of helpers. There is growing evidence that facultatively cooperative breeding systems found in insects are analogous to those in vertebrates in terms of kin-directed helping, ecological constraints as selective pressures on independent breeding, helper effect and inheritance of breeding position (6). Some facultatively cooperative breeding species with special reference to relative proportions of the two types of breeding units in the same population are listed in Table S2.

The coexistence of both types of breeding units indicates that the populations may be characterized by $rb = c$. Nevertheless, inconsistence between the expression of breeding social organizations and altruism polymorphism may occur on a few occasions, which will be clarified later.

Eusocial: Breeding units in a population are composed entirely of cooperative groups, known as colonies. As the extreme form of cooperative breeding, a colony often includes one or a few reproductively-active queens or kings and thousands to millions of workers, which as close relatives of the breeders have lost reproductive options for their lifetime. Therefore, a colony is usually very large compared to that of facultatively cooperative insects and vertebrates (usually less than 10 individuals), though some species such as the beetle *Austroplatypus incompertus* have colony size of 6-7 individuals. A colony also has much higher productivity than a cooperative group of facultatively cooperative breeders. Breeders and workers (called castes) in a eusocial colony are morphologically distinct, with the latter being females in some taxa or both sexes in others. Workers assist in brood care and other tasks involved in colony maintenance, such as feeding the breeders and other types of workers (7).

Eusociality is restricted to a few taxonomic groups, largely the class Insecta. The social form has also been reported in some trematode flatworms, spiders, and snapping shrimps. The naked mole rat *Heterocephalus glaber* is thought to be the only eusocial mammal.

A eusocial population is obviously altruism-monomorphic, because altruistic genotypes have gone to fixation so that they are present in all colonies in a population.

Solitarily breeding is not expected to invade the population, thereby making $rb > c$.

Variation in Breeding Social Organization among Taxa. While many taxonomic groups comprise only solitarily breeding species, some other groups such as ants, stingless bees, honey bees and termites include only eusocial species, because their closely related solitary taxa have gone extinct. In contrast, many lineages exhibit partial or full-range variation in the level of sociality. Those phylogenetic patterns reflect evolutionary transitions in sociality through time. For example, eusociality has 3 origins and 12 losses within the subfamily Halictinae (8). Facultatively cooperative breeding has evolved 33 times in 267 avian species (9) and has been lost 82 times in 4707 avian species (10).

Differences in social organization even occur among populations of a single species. It has been known that there is a decrease in colony size but an increase in the proportion of solitary breeders towards high latitudes or altitudes for many spider and insect species (11). In the carrion crow *Corvus corone*, all pairs in the populations of European mainland breed alone, whereas 75% of pairs in the Spanish population have helpers (12).

Potential drivers of the inter- and intra-specific variation in social organization have been attributed to environmental conditions. For short-lived insects, cold climates allow a narrow breeding window during which all individuals in a population are single-brooded, making it impossible for workers to develop (11). In facultatively cooperative breeding insects, there are at least two broods during an annual cycle, which allows the offspring from the earlier broods to act as workers helping rear the following broods. This fact may explain why eusocial lineages mostly live in the tropics. In birds, slow population turnover in warm regions is more likely to prevent some adults from finding breeding vacancies and promote them to join a pair and act as helpers; in contrast, mate shortage as the limitation on independent breeding tends to arise in cold regions where breeding turnover is fast but adult sexual ratios are male-biased (13).

Variability in social organization provides ample testing grounds for our framework in terms of altruism polymorphism based on rb vs. c relations. The evolution and maintenance of sociality can be understood via exploring internal and external factors that affect r, b and c. Compared to previous approaches at the between-species (review in 14) or within-colony scale (15), our framework at the within-population scale may add a new dimension to investigations of social evolution.

Conceptual Difference between Phenotype-based and Genotype-based Polymorphism in Reproductive Altruism. Obviously, solitary and eusocial taxa contain only non-altruism and altruism monomorphism, which correspond well to $rb < c$ and $rb > c$, respectively. We may expect that altruism polymorphism mediated by $rb = c$ should exist in facultatively cooperative breeding systems. Nevertheless, in some particular cases, facultatively cooperative breeding does not necessarily predict the presence of altruism polymorphism. For instance, in a few avian cooperative breeders (e.g. white-winged choughs *Corcorax melanorhamphus*, 16), all breeding units are cooperative but some individuals never help during their life. In contrast, it is likely that all individuals in a population act as helpers but the population contains both solitary and cooperative nests. The inconsistency may be attributed to the difference in scales on which the two concepts rest. Altruism polymorphism by definition means that altruistic and non-altruistic genotypes are both present in a population, thereby being based on an individual scale, whereas social organization is on the breeding unit scale.

Hence, the idea of altruism polymorphism is a simple, convenient tool by which we can analyze the evolution of altruism hidden in various types of breeding social organizations.

An overview of other forms of altruism in nature: A perspective of behavioral polymorphism

In addition to reproductive altruism, a variety of altruistic behaviors have been identified in the animal kingdom. Here, we refer to altruistic behaviors as ones that reduce actors' own fitness to increase the fitness of others. Thus, we do not include reciprocal altruism in which direct benefits are exchanged between the actors and the recipients at the same time or over a period of time (17).

We provide a preliminary summary of cases of these altruistic behaviors reported in the literature (Table S3). These forms of altruism tend to occur between kin, and prove to be facultative with alternative traits coexisting in the same population. In some cases, altruism is directed towards non-kin (18, 19, 20, 21). These non-kin interactions may also be understood from the perspective of behavioral polymorphism because the terms *r*, *b*, and *c* in Hamilton's rule could all be positive, negative or zero (22).

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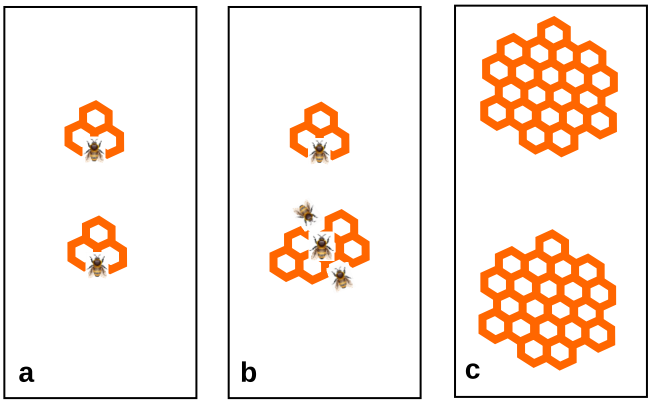

Fig. S1. A sketch showing different types of breeding social organization. a. Solitary: a population consisting completely of solitarily breeding units; b. Facultatively cooperative: a population consisting of both solitarily and cooperatively breeding units; c. Eusocial: a population consisting completely of cooperatively breeding units.

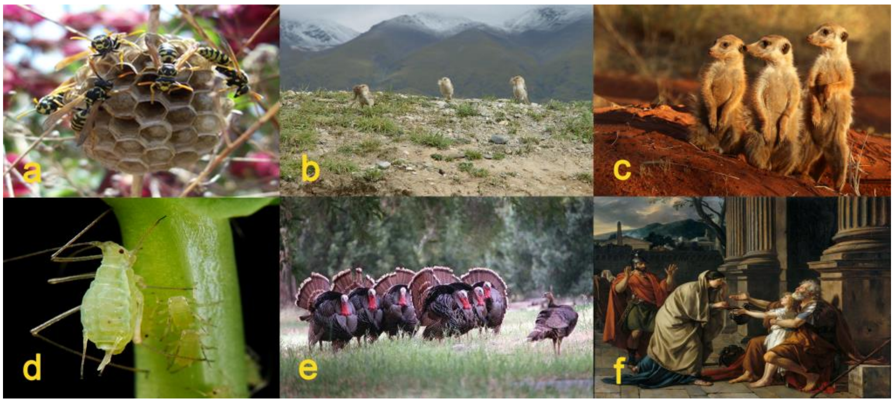

Fig. S2. Making sense of altruism coexisting with non-altruism in nature and humans. Helping to rear offspring of others in facultatively cooperative breeders: a. paper wasps *Polistes dominulus*; b. Tibetan ground tits; c. meerkats *Suricata suricatta*. Several other forms of altruism: d. Adaptive suicide, to reduce the chance of kin being parasitized in pea aphids *Acyrthosiphon pisum*; e. Cooperative courtship, to facilitate mating success of other males in wild turkeys *Meleagris galloparvo*; f. Compassion for others, to give alms to beggars in humans. Photos a-e by Eugene Zelenko, Danhua Ke, Charles Sharp, Shipher Wu, and Kelly Burgess, respectively, and the painting f by Jacques-Louis David.

Table S1. The distribution of breeding social organizations across the animal kingdom

Class	Order	Family or subfamily	No. of described species in the world	Solitary	Facultative	Eusocial
Invertebrates						
Digenea (trematode)[1]			6000	most	most	a few
Malacostraca[2]	Decapoda	Alpheidae (shrimps)	1120	most	a few	a few
Arachnida[3]	Araneae (spiders)		40700	most	a few	a few
Insecta[4, 5, 6, 7, 8]	Hymenoptera	Formicidae (ants)	16000	0	0	all
		Apidae (bees)	5700	many	many	many
		Vespidae (wasps)	5000	many	many	many
		Crabronidae (wasps)	9000	many	a few	0
		Halictinae (bees)	2500	many	830	0
		Apidae (bees)	5700	many	a few	a few
	Isoptera (termites)		2600	a few	a few	most
	Hemiptera	Aphididae (aphids)	2280	most	a few	a few
	Thysanoptera	Thripidae (thrips)	2000	most	a few	a few
	Coleoptera (beetles)		400000	most	1	1
Vertebrates						
Osteichthyes[9]	Perciformes	Cichlaidae (cichlids)	2000	most	a few	0
Aves (birds) [10]			10000	most	900	0
Mammalia (mammals) [11]			5420	most	100	1

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Table S2. A summary showing the relative proportion of solitarily and cooperatively breeding units in a population of facultatively cooperative breeding insects and vertebrates

Scientific name	No. of breeding units	% cooperatively breeding unit	Sources
Insects			
Myrmecocystus mimicus	96	53.1	Bartz & Holldobler 1982
Polistes fuscatus	38	2.6	Eberhard 1969
Polistes canadensis	20	25.0	Eberhard 1969
Xylocopa virginica	23	65.2	Prager 2014
Ropalidia marginata	48	77.1	Premnath *et al.* 1996
Ceratina nigrolateralis	32	6.7	Rehan *et al*. 2009
Neoceratina dentipes	20	5.0	Rehan *et al*. 2009
Pithitis smaragdula	5	20.0	Rehan *et al*. 2009
Ceratina australensis	378	12.4	Rehan *et al.* 2011
Lasioglossum malachurum	52	21.2	Richards *et al*.2005
Ceratina japonica		20.0	Sakagami & Maeta 1984
Megalopta genalis	113	65.5	Kapheim *et al*. 2013
Polistes metricus	64	21.9	Metcalf & Whitt 1977
Lasius niger		18.0	Sommer & Holldobler 1995
Xylocopa sulcatipes	124	43.5	Stark 1992
Exoneura nigrescens	46	19.6	Zammit *et al*. 2008
Fish			
Neolamprologus pulcher	60	95.0	Taborsky & Limberger 1981, Taborsky
Birds			
Rhea americana	35	23.0	Codenotti & Alvarez 1997
Tetraophasis szechenyii	68	64.7	Xu *et al*. 2011
Opisthocomus hoazin	364	59.0	Strahl 1988
Gypaetus barbatus	92	15.2	Bertran & Margalida 2002
Haliaeetus vociferoides	95	42.0	Tingay *et al*. 2002
Neophron percnopterus	37	5.4	Tella 1993
Parabuteo unicinctus	64	84.4	James & Mannan 1991
Buteo galapagoensis	32	68.8	Faaborg *et al*. 1980
Melierax canorus	117	13.7	Malan 2004
Monias benschi	108	56.5	Seddon *et al*. 2003
Porphyrio porphyrio	93	92.0	Craig & Jamieson 1990
Psophia leucoptera	88	100.0	Sherman 1995
Rhynochetos jubatus	38	89.5	Theuerkauf *et al*. 2009

Gallinula chloropus	97	12.4	Gibbons 1986
Gallinula mortierii	106	54.7	Goldizen *et al*. 1998
Vanellus chilensis	23	47.8	Saracura *et al*. 2008
Eclectus roratus	34	58.8	Heinsohn & Legge 2003
Myiopsitta monachus	15	20.0	Eberhard 1998
Pyrrhura orcesi	35	74.0	Ridgely & Robbins 1988
Coracopsis vasa	15	100.0	Ekstrom *et al*. 2007
Crotophaga sulcirostris	171	76.0	Koford *et al*. 1990
Guira guira	39	71.8	Lima *et al*. 2011
Crotophaga ani	71	100.0	Grieves *et al*. 2014
Crotophaga major	87	8.0	Riehl & Jara 2009
Ceryle rudis	59	45.8	Reyer 1990
Dacelo novaeguineae	131	66.7	Legge & Cockburn 2000
Merops apiaster	239	19.0	Lessells 1990
Merops bullockoides	187	49.7	Emlen & Wrege 1988
Merops bulocki	96	28.1	Fry 1972
Merops leschenaulti	3	33.3	Burt 2002
Merops orientalis	24	37.5	Sridhar & Karanth 1993
Merops ornatus	180	45.0	Boland 2004
Merops philippinus	19	42.0	Burt 2002
Penelopides exarhatus	2	100.0	O'brien 1997
Phoeniculus damarensis	22	100.0	Plessis *et al*. 2007
Phoeniculus purpureus	189	90.5	Ligon 1990
Todiramphus cinnamominus	57	54.5	Kesler & Haig 2007
Tanysiptera sylvia	71	7.0	Legge & Heinsohn 2001
Colaptes campestris	26	42.0	Dias *et al*. 2013
Semnornis ramphastinus	28	62.0	Restrepo & Mondragón 1998
Picoides borealis	93	46.0	Lennartz *et al*. 1987
Acanthisitta chloris	105	10.5	Sherley 1990
Acrocephalus sechellensis	657	29.0	Richardson *et al*. 2002
Acrocephalus vaughani	22	36.0	Brooke & Hartley 1995
Alophoixus pallidus	183	60.1	Sankamethawee *et al*. 2010, 2011
Aphelocoma coerulescens	545	55.0	Woolfenden & Fitzpatrick 1990
Babax waddelli	10	40.0	Lu 2004
Bubalornis niger	137	100.0	Winterbottom *et al*. 2001
Calocitta formosa	56	52.0	Innes & Johnston 1996
Campylorhynchus griseus	90	30.0	Austad & Rabenold 1986
Campylorhynchus nuchalis	230	67.4	Rabenold 1990
Climacteris affinis	26	34.6	Radford 2004
Climacteris erythrops	20	65.0	Noske 1991

Climacteris picumnus	102	38.2	Doerr & Doerr 2006
Climacteris rufus	90	59.0	Luck 2001
Corcorax melanorhamphos	186	98.9	Rowley 1978
Corvus brachyrhynchos	115	30.0	Caffrey 1992
Corvus corone	236	75.0	Baglione *et al*. 2002
Cyanocorax beecheii	36	81.0	Raitt *et al*. 1984
Cyanocorax chrysops	6	100.0	Uejima *et al*. 2012
Cyanocorax morio	46	100.0	Williams & Rabenold 2005
Cyanopica cyanus	110	49.1	Valencia *et al*. 2003
Eopsaltria georgiana	258	70.0	Russell *et al*. 2004
Erythropygia coryphaeus	427	15.0	Lloyd *et al*. 2009
Garrulax perspicillatus	19	100.0	Wang 2011
Gymnorhina tibicen	12	100.0	Finn & Hughes 2001
Gymnorhinus	341	8.0	Marzluff & Balda 1990
Lamprotornis pulcher	36	97.2	Wilkinson 1982
Lamprotornis superbus	352	91.0	Rubenstein 2007
Lanius excubitoroides	82	81.7	Zack 1986
Malurus coronatus	73	46.6	Kingma *et al*. 2010
Malurus cyaneus	63	36.5	Nias & Ford 1992
Malurus elegans	398	83.0	Russell & Rowley 2000
Malurus leucopterus	37	48.6	Rowley & Russell 1995
Malurus melanocephalus	604	20.0	Varian-Ramos *et al*. 2010
Malurus splendens	226	65.0	Russell & Rowley 1988
Manorina melanophrys	31	100.0	Clarke *et al*. 2002
Melanerpes formicivorus	354	76.5	Koenig & Stacey 1990
Melanerpes formicivorus	164	40.2	Koenig & Stacey 1990
Melanerpes formicivorus	32	14.6	Koenig & Stacey 1990
Mimus parvulus	450	34.0	Curry & Grant 1989
Myrmecocichla formicivora	87	74.7	Barnaby 2012
Neothraupis fasciata	71	32.4	Manica & Marini 2012
Philetairus socius	94	58.5	Covas *et al*. 2006
Phyllastrephus cabanisi	103	37.9	Callens 2012
Pomatostomus ruficeps	90	94.0	Browning *et al*. 2012
Pomatostomus temporalis	75	86.7	Eguchi *et al*. 2007
Prunella collaris	96	44.8	Nakamura 1998
Prunella modularis	208	70.2	Davies 1986
Psaltriparus minimus	97	35.0	Sloane 1996
Pseudonigrita arnaudi	68	23.9	Bennun 1994
Pseudopodoces humilis	159	28.0	Lu *et al*. 2011
Schetba rufa	220	37.3	Eguchi *et al*. 2002

Sericornis frontalis	169	54.0	Magrath & Whittingham 1997
Sialia mexicana	741	7.4	Dickinson *et al*. 1996
Struthidea cinerea	61	100.0	Woxvold *et al*. 2006
Stipiturus malachurus	48	8.0	Maguire & Mulder 2004
Lichenostomus melanops	7	28.6	Franklin *et al*. 1995
Manorina melanocephala	35	100.0	Poldmaa *et al*. 1995
Notiomystis cincta	30	26.7	Castro *et al*. 1996
Daphoenositta chrysoptera	28	82.1	Noske 1998
Chaetops frenatus	35	34.3	Holmes *et al*. 2002
Plocepasser mahali	132	66.7	Harrison *et al*. 2013
Ramphocinclus brachyurus	112	34.8	Temple *et al*. 2009
Sitta pusilla	347	19.7	Cox & Slater 2007
Sitta pygmaea	141	39.7	Sydeman *et al*.1988
Turdoides bicolor	181	94.5	Ridley & Raihani 2008
Turdoides caudata	20	50.0	Gaston 1978a
Turdoides squamiceps	19	89.5	Zahavi 1990
Turdoides striata	30	100.0	Gaston 1978b
Yuhina brunneiceps	69	97.1	Yuan *et al*. 2004
Malurus pulcherrimus	121	27.0	Rowley & Russell 2002
Corvinella corvina	18	100.0	Grimes 1980
Eopsaltria australis	29	27.6	Debus 2006
Cisticola chiniana	17	88.2	Carlson 1986
Acrocephalus melanopogon	25	68.0	Blomqvist *et al*. 2005
Acrocephalus baeticatus	65	12.0	Eising *et al*. 2001
Mimus macdonaldi	53	67.9	Lippke 2008
Catharus bicknelli	18	78.0	Goetz *et al*. 2003
Loxioides bailleui	25	24.0	Patch-Highfill 2008
Calcarius pictus	23	82.6	Briskie *et al*. 1998
Hypopyrrhus	27	100.0	Ocampo *et al*. 2012
Agelaioides badius	20	18.0	Fraga 1991
Parus fasciiventer	49	61.0	Shaw *et al*. 2015
Aegithalos glaucogularis	21	42.9	Li *et al*. 2014
Aegithalos concinnus	50	20.0	Li *et al*. 2012
Garrulax perspicillatus	24	79.2	Wang 2011
Mammals			
Leontopithecus rosalia	211	84.4	Dietz & Baker1993
Saguinus midas	7	57.1	Thorington 1968
Saguinus mystax	18	88.9	Garber *et al*.1984
Castor canadensis	23	52.2	Svendsen 1980

Cryptomys hottentotus	7	57.1	Spinks *et al*. 2000
Cryptomys mechowi	6	100.0	Scharff *et al*. 2000
Cryptomys zechi	28	53.6	Yeboah & Dakwa 2002
Heterocephalus glaber	1	100.0	Jarvis 1981
Rhabdomys pumilio	14	85.7	Schradin & Pillay 2004
Meriones unguiculatus	9	44.4	Agren *et al*. 1989
Microtus ochrogaster	243	15.6	Getz & Hofmann 1986
Microtus pinetorum	20	65.0	FitzGerald & Madison 1983
Peromyscus californicus	27	29.6	Wolff 1994
Peromyscus polionotus	848	7.1	Smith 1966
Alopex lagopus	13	46.2	Strand *et al*. 2000
Canis aureus	19	57.9	Moehlman 1987
Canis latrans	8	62.5	Bekoff & Wells 1986
Canis lupus	24	62.5	Harrington *et al*. 1983
Canis mesomelas	15	73.3	Moehlman 1979
Canis simensis	61	90.2	Zubiri & Gottelli 1995
Helogale parvula	170	99.0	Rood 1990
Lycaon pictus	26	100.0	Fuller *et al*. 1992
Suricata suricatta	9	100.0	Doolan & Mcdonald 1997
Mungos mungo	14	100.0	Cant 2000

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Table S3. A preliminary summary of altruistic behaviors in the context of non-alloparenting in natural populations

Type	Description of altruists' behavior	Taxon and sources
Cooperative courtship	Aggregate in lek to facilitate mating success of related males at the expense of sacrificing their own mating opportunities	Prairie mole cricket *Gryllotalpa major*[1], Black grouse *Tetrao tetrix*[2], Wild turkey *Meleagris galloparvo*[3], Peafowl *Pavo cristatus*[4], some manakins[5, 6, 7, 8, 9]
Egg dumping	Undertake the additional costs of parental care to increase reproductive success of kin parasites	Lace bug *Gargaphia solani*[10], some waterfowl species[11]
Anti-predatory or parasite alarm pheromone	Release costly chemical secretion to alert related individuals	Social aphids[12]
Anti-predatory guard	Usually act as sentinels to protect kin against predation	Some birds and mammals[13]
Killing parasite offspring	Kill oppressors' offspring to reduce raiding pressure on related host colonies nearby	Social ants *Temnothorax* spp.[14, 15]
Adaptive suicide	Increase the probability of dying by dropping off plants to reduce the chance of kin to be parasitized	Pea aphid *Acyrthosiphon pisum*[16]
Larva cannibalism	Abandon to eat related larva but eat those least related	Tiger salamander *Ambystoma tigrinum*[17], Spadefoot toad *Spea* spp.[18]

1. Keane *et al*. 2016; 2. Lebigre *et al*. 2014; 3. Krakauer 2005; 4. Petrie *et al*. 1999; 5. Shorey *et al*. 2000; 6. Loiselle *et al*. 2006; 7. McDonald & Potts 1994; 8. DuVal 2007; 9. Concannon *et al*. 2012; 10. Tallamy 2005; 11. Eadie & Lyon 2011; 12. Mondor & Messing 2007; 13. Caro 2005; 14. Pamminger *et al*. 2014; 15. Czechowski & Godzinska 2015; 16. McAllister & Roitberg 1987; 17. Pfennig & Collins 1993; 18. Pfennig & Frankino 1997.

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